



# Macroecology, global change and the shadow of forgotten ancestors

José Alexandre Felizola Diniz-Filho\* and Luis Mauricio Bini

Departamento de Biologia Geral, ICB,  
Universidade Federal de Goiás, CP 131,  
74.001-970, Goiânia, GO, Brazil

\*Correspondence: José Alexandre F. Diniz-Filho, Departamento de Biologia Geral, ICB, Universidade Federal de Goiás, Goiânia, GO 74001-970, Brazil.  
E-mail: diniz@icb.ufg.br

## ABSTRACT

Many recent studies have evaluated how global changes will affect biodiversity, and have mainly focused on how to develop conservation strategies to avoid, or at least minimize, extinctions due to shifts in suitable habitats for the species. However, these complex potential responses might be in part structured in phylogeny, because of the macroecological traits underlying them. In this comment, we review recent analytical developments in phylogenetic comparative methods that can be used to understand patterns of trait changes under environmental change. We focus on a partial regression approach that allows for partitioning the variance of traits into a fraction attributed to a pure ecological component, a fraction attributed to phylogenetically structured environmental variation (niche conservatism) and a fraction that may be attributed to phylogenetic effects only. We then develop a novel interpretation for linking these components for multiple traits with potential responses of species to global environmental change (i.e. adaptation, range shifts or extinctions). We hope that this interpretation will stimulate further research linking evolutionary components of multiple traits with broad-scale environmental changes.

## Keywords

Comparative methods, global change, macroecology, partial regression, phylogenetic autocorrelation, phylogeny.

*... Granted, prophecy is a lost art and we are not vouchsafed an unclouded view of our future. Indeed, we are almost wholly ignorant of what is coming. But by what right, what argument can pessimism be justified? Whatever else may be hidden in those shadows, our ancestors have bequeathed us – within certain limits, to be sure – the ability to change our institutions and ourselves. Nothing is preordained.*

Sagan & Druyan (1992)

## INTRODUCTION

Pervasive evidence of a human influence on the functioning of the biosphere is growing steadily (Vitousek *et al.*, 1997; Sala *et al.* 2000). Multiple scenarios of future worlds based on these human-induced changes can be derived, although forecasts are uncertain, because they depend on how human societies will continue (or not) to create positive feedbacks that increase the magnitude of global changes (see Cohen, 1995; Allen *et al.*, 2000; Bousquet *et al.*, 2006; Schaphoff *et al.*, 2006).

Many recent studies have evaluated how these global changes will affect biodiversity, mainly focusing on climatic effects (Walther *et al.* 2002; Parmesan & Yohe, 2003; Perry *et al.*, 2005; Araújo & Rahbek, 2006) and on how to develop conservation strategies that minimize the likelihood of species extinctions due to geographical shifts in habitats (Hannah *et al.*, 2002; Miles *et al.*, 2004; Araújo *et al.*, 2004, 2005; Thuiller *et al.*, 2006). These studies usually evaluate climatic determinants of species' geographical ranges, using niche-based modelling approaches (see Araújo & Guisan, 2006), and then project these ranges into future environments, predicted by alternative scenarios of climatic change (see e.g. Thomas *et al.*, 2004). Other characteristics, such as body size and population density, are also used to predict the responses of species to these changes (e.g., Millien *et al.*, 2006). Thus, it is possible to evaluate how these macroecological components and their emergent properties, like species richness, patterns in biotic interactions and functional diversity within communities and ecosystems, will be driven by changing environments under adaptation or community sorting processes (Thuiller *et al.*, 2004; Araújo *et al.* 2005, 2006; Schröter *et al.*, 2005; Araújo & New, 2006).

Although the short-term responses of species to these environmental changes can be captured in part by niche-based modelling strategies, they ultimately depend on multiple intrinsic and extrinsic factors and will generate three basic outcomes at the species level: adaptation, extinction and geographical range shifts (Schlensinger *et al.*, 2001). This is expected if geographical ranges reflect a spatial structure of the response of species to environmental factors that is actually mediated by more complex interactions among physiological, ecological, life-history and morphological traits (Herrera, 1992; Webb *et al.*, 2002; Ackerly, 2003).

For example, species responses to climatic change may not always result in shifts (displacement, contraction or expansion) in their geographical range. Sometimes responses may involve local adaptive responses of traits that allow species to survive in the changing environment. On the other hand, constraints to adaptation and limiting dispersal throughout the new environmental space can drive species to extinction, depending on how these traits are linked to fitness (e.g. Martínez-Meyer *et al.*, 2004). Finally, when dispersal is not restricted by barriers, shifts in geographical range may be forecast. It is also interesting to note that even dispersal distances may change in response to changing climatic conditions (Møller *et al.*, 2006).

Additionally, these complex responses might be in part phylogenetically structured, evolving under different models of evolution (Martins & Hansen, 1996; Freckleton *et al.*, 2002; Garland *et al.*, 2005). Thus, comparative phylogenetic methods developed over the last 20 years to understand the evolutionary components of traits could be used to understand the responses of traits (and their emergent properties, such as geographical ranges and species richness) to climatic changes. In this comment, we review some recent analytical developments in phylogenetic comparative methods that can be used to understand the patterns of change of traits under environmental changes. We then provide a novel interpretation linking the ecological and phylogenetic components of trait variation with the potential responses of species to global environmental changes.

## COMPARATIVE METHODS AND THE PARTITION OF PHYLOGENETIC AND ADAPTIVE COMPONENTS

There are now several methods that can be used to incorporate phylogenetic structure into data analyses (see Harvey & Pagel, 1991; Gittleman & Luh, 1992; Martins & Hansen, 1996; Pagel, 1999; Garland *et al.*, 2005). In some of these comparative methods, the total variation ( $T$ ) of a trait  $Y$  measured in a group of species can be decomposed into phylogenetic ( $P$ ) and specific ( $S$ ) components, so that  $T = P + S$ . Cheverud *et al.* (1985) originally proposed this partitioning approach and used an autoregressive model (ARM) to obtain components  $P$  and  $S$  (see also Gittleman & Kot, 1990; Martins, 1996). In this model,  $Y$  is given by

$$Y = \rho WY + \epsilon$$

where  $W$  is a weighing matrix expressing phylogenetic structure and  $\epsilon$  is the residual term. The autoregressive coefficient  $\rho$

measures the relationship between observed and estimated values of  $Y$ , and the  $R^2$  of this regression model provides an estimate of the phylogenetic signal (or phylogenetic correlation) in  $Y$ . The term  $\rho WY$  defines the phylogenetic component  $P$ , whereas the residuals  $\epsilon$  are the unique part of  $Y$  that evolved independently in each species, the 'ecological' component  $S$ . Thus, trait  $Y$  in each species now has a value for the phylogenetic component and a value for the specific component.

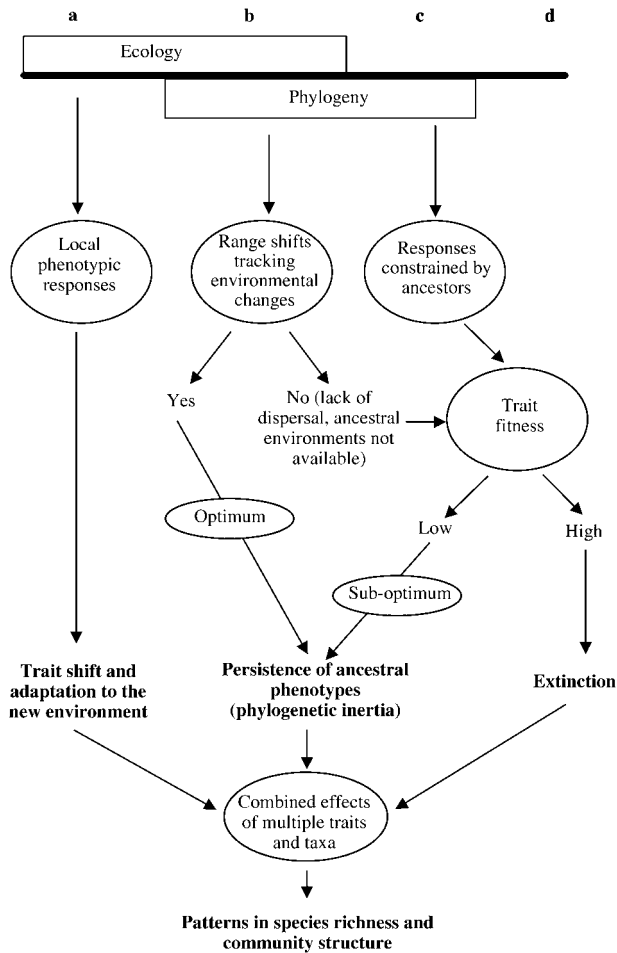
More recently, Diniz-Filho *et al.* (1998) proposed a technique called phylogenetic eigenvector regression (PVR) to perform the same partitioning, but using a more general approach based on multivariate analysis (i.e. principal coordinate analysis; see Legendre & Legendre, 1998). The idea is that phylogeny can be expressed as a set of orthogonal vectors obtained by eigenanalysis of a phylogenetic distance matrix. These vectors can then be used as predictors of  $Y$  in any form of linear model (see also Borcard & Legendre, 2002, and Diniz-Filho & Bini, 2005, for analogous applications in a spatial context). Thus, PVR follows the standard framework of general linear models, so that

$$Y = X\beta + \epsilon$$

where  $X$  is a matrix with the orthogonal eigenvectors (filters) of the double-centred phylogenetic distance matrix  $D$ , and  $\beta$  are partial regression coefficients. Since phylogenetic structure was incorporated in the model structure ( $X\beta$ ), the residual term  $\epsilon$  is independent of this structure and is an estimate of the ecological component  $S$ . As in ARM, the  $R^2$  of this multiple regression model provides an estimate of the phylogenetic signal in the data, but the PVR allows more flexibility in analytical designs.

In practice, PVR and ARM are usually applied independently to various traits. For example, one may be interested in estimating the correlation between a trait  $Y$  (e.g. body size) and an ecological or life-history trait  $X$  (e.g. geographical range size) that is independent of phylogenetic structure (Martins *et al.*, 2002; Diniz-Filho & Tôrres, 2002). In this case, this correlation is calculated using the residual terms  $\epsilon_Y$  and  $\epsilon_X$ , which provides an estimate of the 'input correlation' between traits (*sensu* Martins & Garland, 1991), the same parameter estimated by the well-known Felsenstein's (1985) phylogenetic contrasts method.

Recently, Desdevices *et al.* (2003) expanded the theoretical framework of partitioning trait variation, showing that part of the variation attributed to phylogeny (estimated by PVR), previously interpreted as a purely non-adaptive component, could also include adaptive variation if predictor variables are also structured in the phylogeny, in a phenomena called 'phylogenetic niche conservatism' by Harvey & Pagel (1991) (see also Westoby *et al.*, 1995; recent reviews and applications are also provided by Wiens & Donoghue, 2004 and Wiens & Graham, 2005). This is achieved by using a partial regression to obtain a fraction of the trait's variance that contains a purely ecological component [ $a$ ], a fraction [ $b$ ] that is the phylogenetically structured environmental variation (the niche conservatism) and a fraction [ $c$ ] that may be attributed only to phylogeny. The unexplained variation is expressed by a fraction [ $d$ ] (see Fig. 1). Thus, using this partitioning approach, we can evaluate



**Figure 1** A conceptual scheme linking trait components obtained by Desdevises *et al.*'s (2003) method (see also Westoby *et al.*, 1995) and some potential scenarios for species' change under global change. In Desdevises *et al.*'s (2003) method, the total variation in a trait *Y* can be partitioned into a purely ecological component [*a*], containing the part of variation that is correlated with ecological variation but is not phylogenetically structured, a fraction [*b*] that is the phylogenetically structured environmental variation (the shared component indicating the magnitude of niche conservatism) and a fraction [*c*], which is not correlated with the environment but is phylogenetically structured. The component [*d*] is the unexplained variation. These components can be related to the extinction of species, local adaptations, or the persistence of traits in new environments in either optimal or suboptimal conditions. 'Trait fitness' refers to the relationship between trait variation and environmental conditions, or the adaptive value of traits, whereas range shifts actually include displacement, expansion and contraction processes (see text for details).

simultaneously the adaptive response expressing the input correlation between ecological traits (the component [*a*]) and the amount of phylogenetic signal in *Y* (the component [*c*]). More importantly, it might be possible to use these components of trait variation among species to understand their potential responses in a changing environment, as attempted in the interpretation developed below.

### LINKING EVOLUTIONARY COMPONENTS OF TRAIT VARIATION AND GLOBAL CHANGES

After understanding how variation in species traits can be partitioned into multiple components, we can establish which of these components in a given trait (e.g. functional traits, or a 'key trait'; see Ackerly *et al.*, 2006), or combination of traits, might be associated with the responses of different species to environmental changes, by multiple tracks (see Schlensinger *et al.*, 2001) (Fig. 1). The idea is to discuss the multiple tracks by which each partitioned component of trait variation ([*a*], [*b*] and [*c*]) can be associated with a potential outcome for a given species (adaptation, range shifts or extinction) under global change.

The component [*a*] refers to independent responses of species' traits to ecological predictors, regardless of their values in other species and in the ancestors. Thus, a species with a high value for the component [*a*] would quickly respond to environmental changes by evolving adaptations in the trait that might ensure the persistence of the species without geographical range shifts (e.g. Rodríguez-Trelles *et al.* 1998). For example, if the environment gets warmer in a given part of the range of a species then, under Bergmann's rule (see Ashton *et al.*, 2000; Blackburn & Hawkins, 2004, and Rodríguez *et al.*, 2006, for recent reviews), its body size could decrease as an adaptive response of local populations to the new environment (see Millien *et al.*, 2006). Alternatively, independently of the intrinsic genetic component associated with [*a*], local persistence would be achieved by phenotypic plasticity (Via *et al.*, 1995), a property of genotypes in producing, via reaction norms, different phenotypes when influenced by different environments (Potvin & Tousignant, 1996).

On the other hand, the [*b*] component potentially reflects niche conservatism (Wiens & Donoghue, 2004; Wiens & Graham, 2005). This component [*b*] is part of the phylogenetic structure because variation is inherited from ancestors of the species, as the current species retain the same ancestral niches. Although it is difficult to obtain fitted values of this component for each species, we expect that, under climatic change, species with a higher value for the shared variance component are those in which current placement is strongly determined by the phylogenetic structure of environmental variation in the lineage. A high value in this component may then be used to explain why there are shifts in geographical ranges, tracking the environment in which the species, or its ancestor, originally evolved. Note that the term 'range shift' is used here in a general sense, and actually includes displacement, expansion and contraction. This also provides a potential difficulty for future empirical studies testing the interpretation discussed here, since extreme range contraction will lead to extinction too.

The interpretation of component [*b*] as niche conservatism assumes that a causal relationship between phylogeny and environment exists for the clade and generates the shared term. Under this reasonable assumption there is a compelling theoretical reason to expect shifts in geographical range under climatic changes, as many papers try to forecast (Parmesan *et al.*, 1999; Martínez-Meyer *et al.*, 2004; Araújo *et al.*, 2005; Thuiller *et al.*, 2006; Martínez-Meyer & Peterson, 2006). Consequently,

higher values for the components [a] and [b] for a species allow its persistence by creating shifts in geographical range location or allowing the evolution of new forms close to range borders, eventually leading to speciation (Thomas *et al.*, 2001; but see Kirkpatrick & Barton, 1997).

However, this may not be the only scenario associated with the component [b], because species will not persist if, after an environmental change, the ancestral environment is no longer available or if dispersal to the regions in which the ancestral environment occurs is unlikely (due to barriers or simply to a low capacity for long-distance dispersal; see Nathan, 2006). If one of these factors prevails, the fate of the species will depend on how the values of the traits under study are linked to 'fitness' (e.g. the adaptive value of traits, *sensu* Ackerly, 2003). If species' current values for the trait studied strongly determine their location in geographical (and environmental) space, we could tentatively say that this trait is strongly linked with fitness in local populations, in current environmental conditions. So, in the absence of range shifts, the environmental change will probably lead to extinctions. Actually, the complex balance between extinction, niche evolution and conservatism is currently being discussed as a potential mechanism driving broad-scale patterns in species richness (Wiens & Donoghue, 2004; Hawkins *et al.*, 2005; 2006).

On the other hand, in the absence of range shifts, if a trait is not tightly linked to fitness, species can persist locally in the new environmental conditions but will retain trait values that were adapted to the past environment, leaving then in a 'suboptimum' condition in respect to this trait. Thus, trait values will not be entirely in agreement with expectations based on the current environment, and can be explained as reflecting 'phylogenetic inertia' (see Diniz-Filho *et al.*, 1998; Blomberg & Garland, 2002).

Finally, the component [c] expresses 'pure' phylogenetic patterns due to long-term evolutionary constraints and stabilizing selection. However, this component may be due to past adaptive events of niche conservatism that, after a while, become 'inertial'. Because past environments can change at different rates and are not precisely tracked by the evolution of traits (as explained regarding component [b]), accumulation over long times of the component [c] may not be 'captured' by the shared variance between ecological and phylogenetic components measured in extant species (see also Hardy, 2006, for a discussion on reconstructing ancestral ecologies). Irrespective of this, if part of the variation in this component becomes important in the current environment, the same scenarios described above for the component [b] apply. A species will persist out of its optimum environment and extinction can be avoided only if the trait's fitness is not too high, so that the current state of the trait will persist by phylogenetic inertia.

Notice that it may be difficult to determine what levels of the adaptive, niche conservatism and phylogenetic components will lead a species through one of the tracks in Fig. 1 because of other confounding effects. Even if a species' trait has a low component [a] (e.g. 5%), this may be 'enough' to allow adaptation, depending on the absolute genetic variance in local populations. For example, although body size usually has a high phylogenetic component (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003) and, therefore,

a relatively low ecological or niche conservatism component, it can respond quickly to environmental change in some situations (see Millien *et al.*, 2006, for a recent review). On the other hand, body size is also widely used as a surrogate for extinction (e.g. Cardillo *et al.*, 2005), reinforcing the idea that the high phylogenetic component might constrain adaptation to new conditions (Purvis *et al.*, 2005). Nevertheless, an evaluation of the possible outcomes (i.e. adaptation, range shifts or extinctions) may be used retrospectively to understand the relationship between the components of these traits and the various scenarios.

Notice that the above interpretation is also dependent on the relationship between rates of environmental change and the potential for adaptive response (i.e. the balance between the intensity of selective pressure and heritable variation in the trait). Even if there is potential for changes in a trait (and species persistence by adaptation), a very rapid environmental change can drive species extinct if geographical range shifts are not possible. Also, range shifts may be a faster way to ensure persistence, whereas adaptation may occur over a longer time-scale, which later allows expansion of the geographical range (see Ackerly *et al.*, 2006).

A final remark with respect to difficulties in testing the interpretations provided above is that species responses will be determined by a complex 'average' response to phylogenetic and adaptive components in all traits (see Herrera, 1992), weighted by genetic variability and the fitness of each trait. This average response must also consider that interactions among traits can generate changes in the relative magnitude of these components. An improved application might be achieved by applying multivariate partition methods, selecting a set of traits that are better related with potential outcomes.

## CONCLUDING REMARKS

We hope that the novel interpretation we have provided will stimulate further research linking the evolutionary components of multiple traits with broad-scale patterns of environmental change (e.g. phylogenetic comparative analyses of range-shift correlates). As previously pointed out, several lines of theoretical investigation, as well as empirical studies, are required to better establish this link. This might also stimulate movement from a retrospective interpretation of trait dynamics, as performed here, towards a more predictive evaluation of the overall responses of species. In a more general sense, we urgently need to understand how species' traits and their interactions within ecological communities drive emergent or aggregate properties at higher hierarchical levels, such as species richness and geographical ranges, which in turn allow evolution and conservatism of ecological niches by a complex combination of speciation and extinction processes in time and space.

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#### BIOSKETCHES

**José Alexandre F. Diniz-Filho** is interested in statistical methods applied to macroecology, evolutionary biology and conservation biology. His current projects involve the application of spatial autocorrelation analysis and phylogenetic comparative methods to understand the ecological processes associated with latitudinal gradients in species richness.

**Luis Mauricio Bini** is interested in statistical methods applied to biodiversity analyses and limnology. His current projects involve the analysis of community concordance.

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